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Genetic Resistance to the White Pine Weevil in Sitka Spruce

by
Cheng C. Ying

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Ministry of Forests

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SUMMARY

Fifteen-year records of weevil attack at Sitka spruce provenance trials revealed large differences among provenances in percent of trees attacked and number of attacks per tree. This provenance variation in weevil attack was repeated in a clonal test, suggesting there is a genetic basis in weevil resistance. On average, provenances from the high weevil hazard zone, as well as those from the hybridization zone, showed a high level of resistance to weevil attack. Two provenances, Haney and Big Qualicum, showed especially high resistance to weevil and were fast growing. These are recommended as seed sources if planting of Sitka spruce in the high weevil hazard zone is considered.

Selection and clonal screening of a large number of putatively resistant trees are in progress, and an estimate of 50 resistant clones will be released for operational use in 1996-97. Use and long-term breeding of genetic resistance are discussed.

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INTRODUCTION

Sitka spruce (*Picea sitchensis*) accounts for only about 2% of the total coastal reforestation in British Columbia, despite its stumpage price which is the second highest in the province and about twice as high as the average of other species (B.C. Ministry of Forests 1990). Destructive damage caused by the white pine weevil (*Pissodes strobi*) to plantation Sitka spruce is the major deterrent to reforestation with this species in coastal British Columbia (MacSiurtain 1981; Alfaro 1982, 1989). Planting is now limited to low weevil hazard areas on the Queen Charlotte Islands, North Vancouver Island, and the outer coast of the mid- and north mainland (Heppner and Wood 1984). None of the control techniques, including shading, clipping, insecticides, or biological control, has proved to be sufficiently effective and practical (Cozens 1983). There is increased interest in genetic control, alone and in combination with other control methods, since the discovery of apparent provenance differences in tolerance of weevil attack (Wood 1987). Selection and clonal screening of resistant Sitka spruce has been initiated.

Weevil attack in Sitka spruce provenance trials has been periodically recorded. These results indicated that some of the provenances were able to resist or tolerate weevil attack significantly better than others, suggesting the potential of selecting for weevil resistance. To test this potential, a small scale clonal test was established with grafts in 1984. Early results from this clonal test confirmed what had been observed in the provenance trials. Because of these encouraging results, we have started a program of selecting and screening resistant trees from both provenance plantations and natural stands of resistant provenances. Our goal is to produce operational quantities of resistant trees.

The objective of this report is to provide:

1. a brief overview of the Sitka spruce provenance testing program;
2. a summary of results of weevil attack in provenance and clonal tests;
3. a brief account of progress in the selection and clonal screening of resistant trees; and
4. a discussion on the practical implications of using, selecting, and breeding for genetic resistance in the short and long term. A provenance's "resistance (tolerance)" or "susceptibility" is defined according to the number of attacks that it experiences over time, or the percent of trees attacked. These terms do not refer to any mechanism of host-insect interaction.

The Provenance Program

Sitka spruce provenance trials were established from 1973 to 1975 at 14 locations (Figure 1; Appendix 1), involving a total of 43 provenances (Figure 2; Appendix 2) in four series. The first series was planted at five locations on the Queen Charlotte Islands in 1973 and involved 38 Alaskan and British Columbian provenances (Illingworth 1978). Its primary purpose is to guide the selection of seed source in that region. The second series is a single test at Sayward planted in 1974 with the same provenances as in series 1, but with the identity of individual wind-pollinated families maintained (Alfaro and Ying 1990). The latter plantation is intended to provide a preliminary screening of provenances or families for resistance to the white pine weevil. Falkenhagen (1974) described the details of provenance origin and geographic variation in cone, seed, and seedling morphological characteristics. Series 3 and 4 are part of the international co-operative provenance experiment of Sitka spruce, organized by the International Union of Forest Research Organizations (IUFRO). Ten provenances were included in each series, with six overlapping. Four tests in each series were planted in 1975 (Illingworth 1978).

Four sites (Sayward, Head Bay, Kitimat, and Nass [Figure 1]), were heavily attacked by weevil. Weevil attack at Sayward was first recorded in 1981 and a thorough assessment was made in 1988 (number of attacks on each tree, determined by stem defects, were recorded) (Alfaro and Ying 1990). Trees attacked by weevil at Head Bay, Kitimat, and Nass were recorded in 1980 (6th year), 1982, (1983 at Head Bay), 1984, and 1989. The 1989 assessment at these three sites recorded the number of weevil attacks on each tree in the past 5 years (since 1984), using the same method as described by Alfaro and Ying (1990). Beginning in 1990, weevil attack at all sites will be recorded annually for 4-5 years. This profile of individual tree records of weevil attack will supplement the test results from clonal screening, and thus facilitate our ability to make early decisions on the selection of resistant trees.

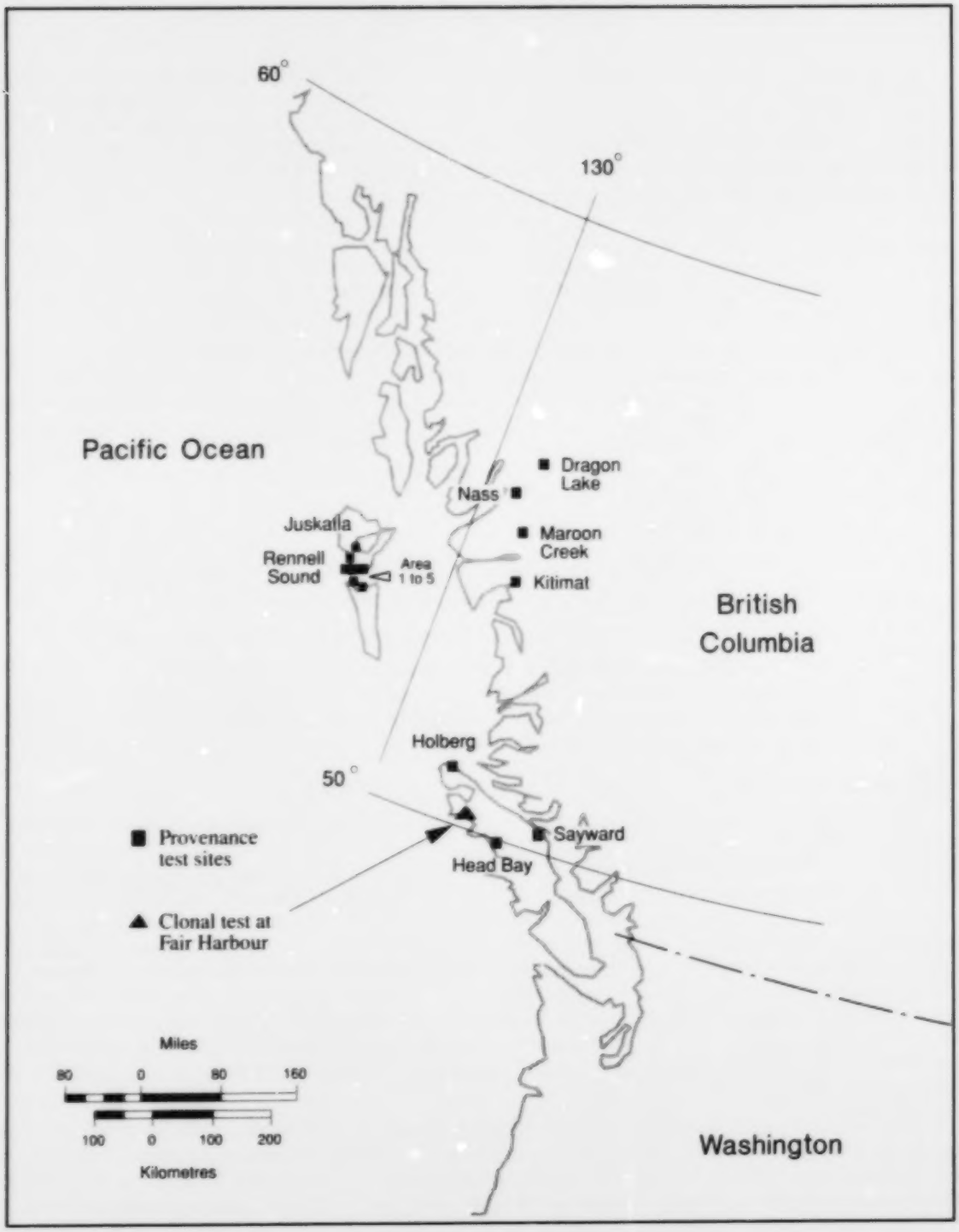

FIGURE 1. Location of Sitka spruce provenance trials and the clonal test for genetic resistance to the white pine weevil.

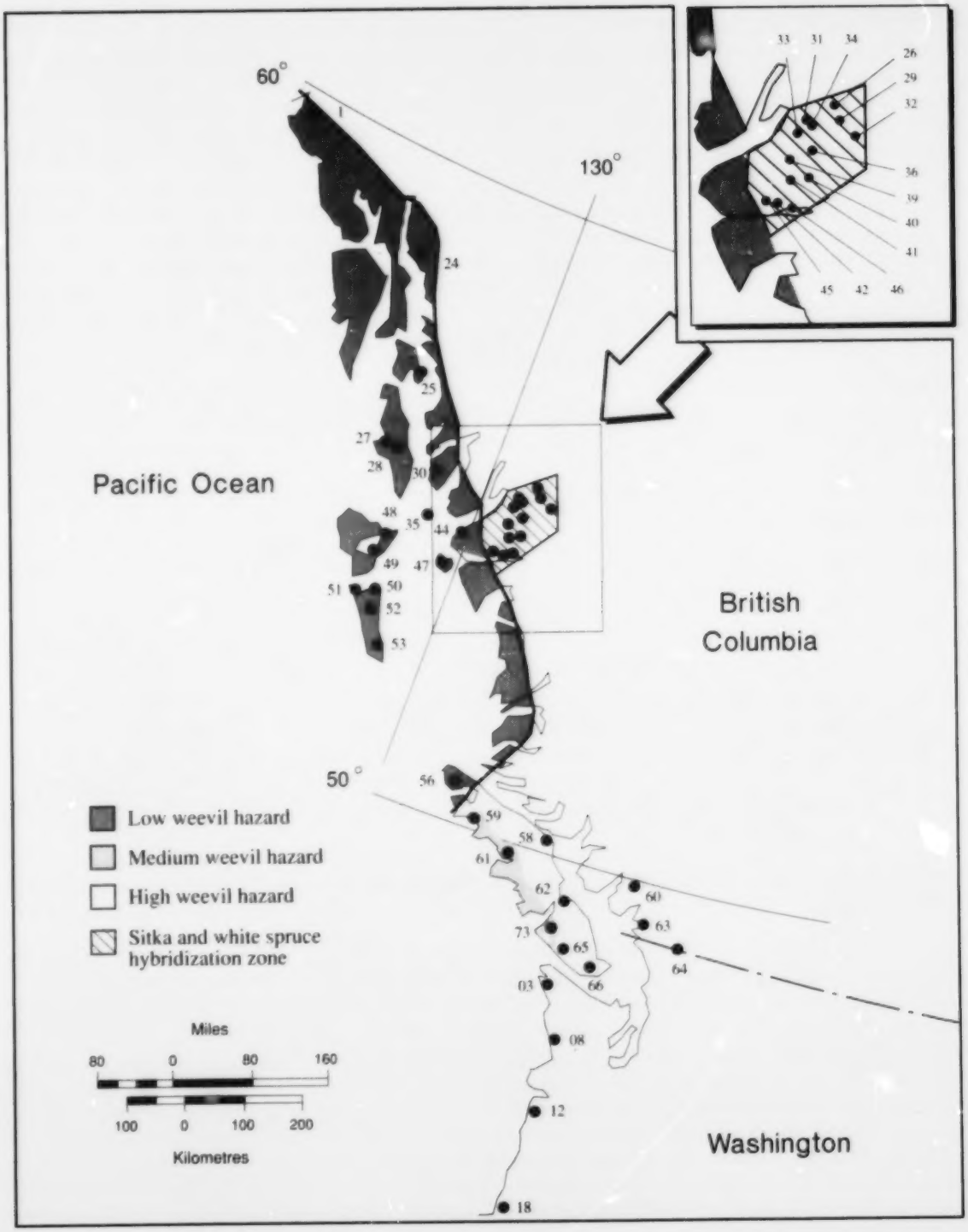

FIGURE 2. Location of Sitka spruce provenances, and the approximate boundaries of low, medium and high weevil hazard zones and Sitka-white hybridization zone.

Clonal Test

Provenance differences in weevil resistance were already obvious when the tests were only 7 or 8 years old. To test the genetic basis of these observed differences, and also the effectiveness of selection for resistant trees in plantations already exposed to severe natural screening of weevil attack, it was decided to establish a small clonal test using grafts. A clonal test can quickly and precisely measure and verify genetic resistance of individuals without the complication of sexual recombination (Gerhold 1966). Grafting is a well-established reliable propagation method.

In 1981, 36 trees from 8 different provenances (Table 1; Figure 2) with varying degrees of weevil resistance at Sayward were selected for the clonal test. Two trees originating from the Green Timbers Sitka spruce plantation[1] were also included. Scions from these trees were collected and grafted at the Cowichan Lake Research Station in 1982. The clonal test was established in 1984 near Fair Harbour (Figure 1) in 16 blocks of one graft per tree (ortet). A total of 640 grafts were planted. Weevil incidence has been closely monitored since the test's establishment.

Weevil Attack at Sayward

Forty-six percent of the trees were attacked when the test was first assessed in 1981 (8 years old). In 1988, the total number of weevil attacks in every tree, determined by recognizable stem defects (minor crook, major crook, and fork), were recorded, and total height and diameter at 1.3 m height were measured. The results are reported in Alfaro and Ying (1990). Provenance means of the number of attacks, percent of trees attacked, and total height are listed in Appendix 3.

TABLE 1. The eight provenances and the Green Timbers (GT) trees included in the clonal test at Fair Harbour

Provenance IUFRO code	Location	Zone[a]	No. of families	No. of trees	No. of attacks in severe patch
32	Kitwanga	X	1	4	1.1
36	Cedarvale	X	1	4	0.8
45	Aberdeen	X	1	4	1.4
51	Moresby Camp	L	1	4	2.5
52	Tasu Creek	L	1	4	1.9
59	Fair Harbour	M	1	4	2.0
63	Haney	H	2	8	0.6
66	Sooke	H	1	4	1.8
GT	Green Timbers	L		2	

[a] L = low, M = medium, and H = high weevil hazard zone (Heppner and Wood 1984); X = Sitka-white spruce hybridization zone (Woods 1988).

The number of attacks per tree averaged 1.5 and ranged from 0 to 7. Twenty-four percent of the trees had never been attacked. The percentage of trees never attacked varied by provenance from 5 to 51%. Variance analysis using a nested model indicated that both provenance and family-in-provenance had a significant effect ($p<0.01$) (Alfaro and Ying 1990).

To examine the geographic pattern of provenance variation in weevil attack, we grouped the provenances into low, medium, and high weevil hazard zones (Heppner and Wood 1984), and a Sitka-white spruce hybridization zone (Woods 1988) (Figure 2; Appendix 2). Variance analyses indicated that the zones accounted for about 50% of the among-provenance variance, and that zonal differences were statistically significant ($p<0.005$) (Table 2). Provenances from the high weevil hazard zone and hybridization zone had a significantly lower number of attacks and lower percent of trees attacked than did those from the low and medium weevil hazard zones (Figure 3). Trees from the high hazard zone, however, grew significantly taller than those from the hybridization zone (Figure 3).

[1] More than 30000 pure Sitka spruce of Queen Charlotte Islands origin were planted near the Green Timbers Nursery of B.C. Ministry of Forests between 1930 and 1935. This plantation was virtually destroyed by weevil, but five trees escaped (Alfaro 1982).

TABLE 2. Variance associated with weevil-hazard zones and provenances within zones, in percent of trees attacked at least once (A), number of attacks per tree (B), number of attacks per tree within severe patches (C), and total height (D)

Source	Df	A		B		C		D	
		MS	VC (%)	MS	VC (%)	MS	VC (%)	MS	VC (%)
Zone	3	743	45[a]	0.87	51[a]	1.03	41[a]	2.26	70[a]
Provenance	29	106	55	0.10	49	0.17	59	0.12	30

[a] Significant at $p<0.005$.

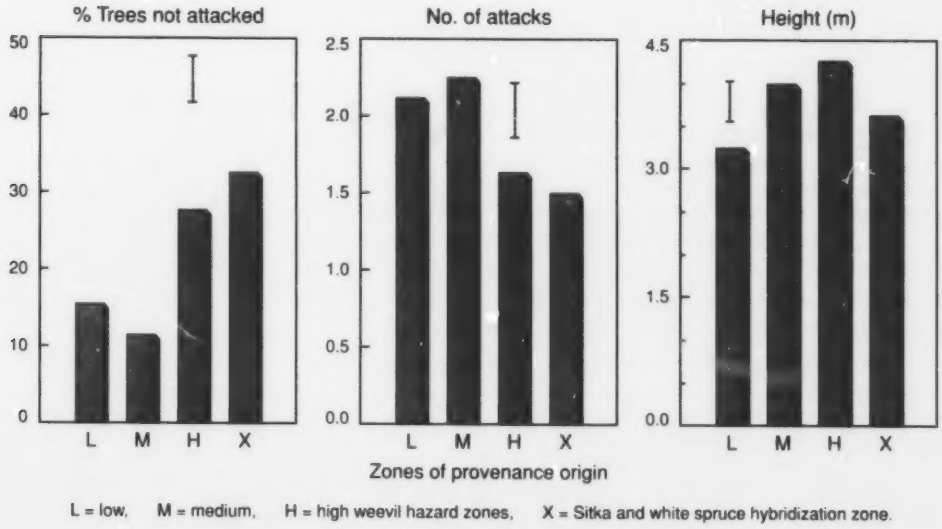

FIGURE 3. Comparison in percent of trees not attacked, number of attacks per tree, and total height among provenances from different zones at Sayward, 15 years after planting. Barred line scaled to 1 LSD at 0.05 level.

Among the seven provenances from the high weevil hazard zone, trees from the Haney provenance had the lowest number of attacks, averaging 0.8 overall and 0.6 within the patches of severe attack, and had the lowest number of trees attacked, 49%. They were also the tallest, averaging 5.5 m. The Squamish provenance showed a high degree of weevil tolerance, with 69% of the trees being attacked. The average number of attacks were 1.2 overall and 0.9 within the severe patches. The Big Qualicum provenance had higher than the plantation average in number of attacks and percent of trees attacked (Appendix 3). This was a rather poor performance compared with the high tolerance of weevil attacks it showed in other sites (discussed below).

Weevil Attack at Head Bay, Kitimat, and Nass

Nass (Figure 1) was the first site attacked by weevil; almost 10% of the trees were attacked 6 years after planting, compared with 4% at Head Bay and less than 1% at Kitimat (Figure 4). Weevil attack increased rapidly at all three sites; in 1989 (15 years after planting), 83.7% of the trees were hit at least once since 1984, varying from 76% at Head Bay to 90% at Kitimat (Appendix 4). The average number of attacks was 1.78, varying from 1.0 attacks at Head Bay to 2.5 at Kitimat (Appendix 4).

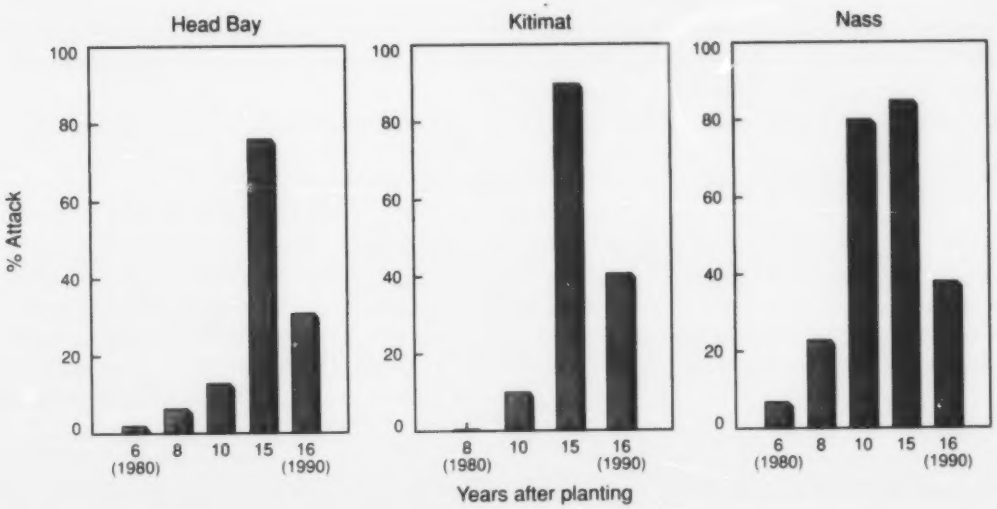

FIGURE 4. Percent of trees attacked at different ages (15-year data are % of trees attacked at least once since 1984) at Nass, Kitimat, and Head Bay.

Provenance differences were large. Among the six provenances tested at all three sites, the Big Qualicum provenance (No. 62) had less than one-quarter of trees attacked and less than half the average number of attacks than other trees (Figure 5). It was also the tallest (Figure 5). At weevil-free sites, trees from the Oregon-Washington coast (Nos. 12 and 3) grew faster than those from Big Qualicum (Illingworth 1978). Obviously, repeated weevil attacks had reduced their height growth.

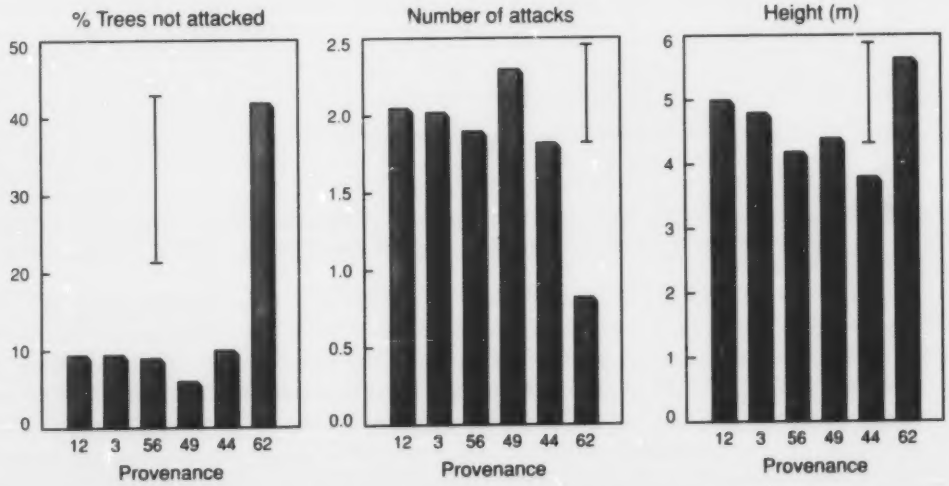

FIGURE 5. Comparison in percent of trees free of weevil attack, of number of attacks per tree, and of total height in 1989 (15-year-old trees) among the six provenances tested at all three sites — Nass, Kitimat, and Head Bay. Barred line scaled to 1 LSD at 0.05 level.

The geographic pattern of provenance variation in weevil attack was generally similar to that observed at Sayward. Provenances from the high weevil hazard zone (Big Qualicum) and the hybridization zone (Nos. 40 and 32) had a significantly lower percent and number of attacks than did others (Appendix 4).

Weevil Attack at the Clonal Test

Only 8 of the 640 grafts died in 1990 after 7 years. This test provided the most evident results of provenance and clonal differences in resistance to weevil attack (Figure 6).

Only three grafts (0.5%) were attacked by weevil in 1986, but it increased rapidly to 22% in 1988, reached 57.3% in 1989, and levelled off to 22.1% in 1990 (Figure 7). In 7 years, 66.7% of the grafts were attacked at least once, and the average number of attacks per graft was 1.03. About 4% of the grafts were attacked three times and one graft attacked four times.

Percentage of grafts free from weevil attack varied by provenance from 1.6 to 89.1% (Figure 8) and the average number of attacks from 0.13 to 1.82 (Figure 9). The Haney provenance (No. 63) was nothing less than remarkable in its ability to resist weevil attack (Figure 6): only 14 of the 128 grafts (10.9%) were attacked and averaged 0.13 attacks per graft. The Sooke provenance (No. 66) (bordering the high and medium hazard zones) was among the least resistant (Figures 8 and 9). Two provenances (Nos. 32 and 36) from the hybridization zone were above average in weevil resistance, and one (No. 45) was among the worst (Figures 8 and 9). Provenance No. 45 may be genetically close to a pure Sitka spruce, judging from its geographic location (Figure 2) (Woods 1988). All three provenances (Nos. 51, 52 and 59) from the low and medium weevil hazard zones were heavily attacked (Figures 8 and 9); 97% of the grafts were attacked and 1.64 attacks occurred per graft. The most important result is that the ranks in provenance differences in number of weevil attacks is almost identical to that observed at Sayward (Table 1).

Only 26% of the grafts originating from the two Green Timbers trees were free of weevil attack (Figure 8), and the average number of attacks per graft was 1.09 (Figure 9). A higher level of resistance was expected of these two trees because the Green Timbers plantation had undergone more than 50 years of exposure to high intensity natural selection. Only five of more than 30000 trees escaped the repeated weevil attack (Alfaro 1982). On the other hand, the seed origin of this plantation was from the Queen Charlotte Islands (Alfaro 1982) where Sitka spruce likely has never been exposed to weevil infestation. Populations originating from these provenances are expected to contain a low frequency of resistant genes in their gene pool. The high susceptibility to weevil of all the Queen Charlotte provenances (Nos. 48 - 53) in all the provenance tests (Table 1; Appendices 3 and 4) seems to support this suggestion. In this clonal test, the Green Timbers trees, although below test average, showed significantly higher resistance than the Queen Charlotte provenances (Nos. 51 and 52). This seems to indicate the effectiveness of natural screening in a plantation of heavy weevil infestation.

The variance component for provenance was 10 times larger than that for clones-within-provenances in number of attacks, and five times larger in percent of weevil-free grafts (Table 3). The reason is probably that clones were from only one or two families in each provenance (Table 1), rather than that genetic variation within provenances in weevil resistance was lacking.

The significance of the results is that differences in weevil resistance observed in provenance tests have been repeated in this clonal test. This is a strong indication of the genetic basis in resistance to weevil attack.

TABLE 3. Variance associated with provenances and clones within provenances, in total and average number of attacks per grafts, and percent of grafts not attacked in 7 years at Fair Harbour

Source	Df	No. of attacks				% Grafts free of weevil	
		Total		Average			
		MS	VC (%)	MS	VC (%)	MS	VC (%)
Provenance	8	30.5	50*	1.91	50*	879	84*
Clone (provenance)	29	1.2	5*	0.08	5*	166	16
Error	598	0.4	45	0.02	45		

* Significant at $p<0.001$.

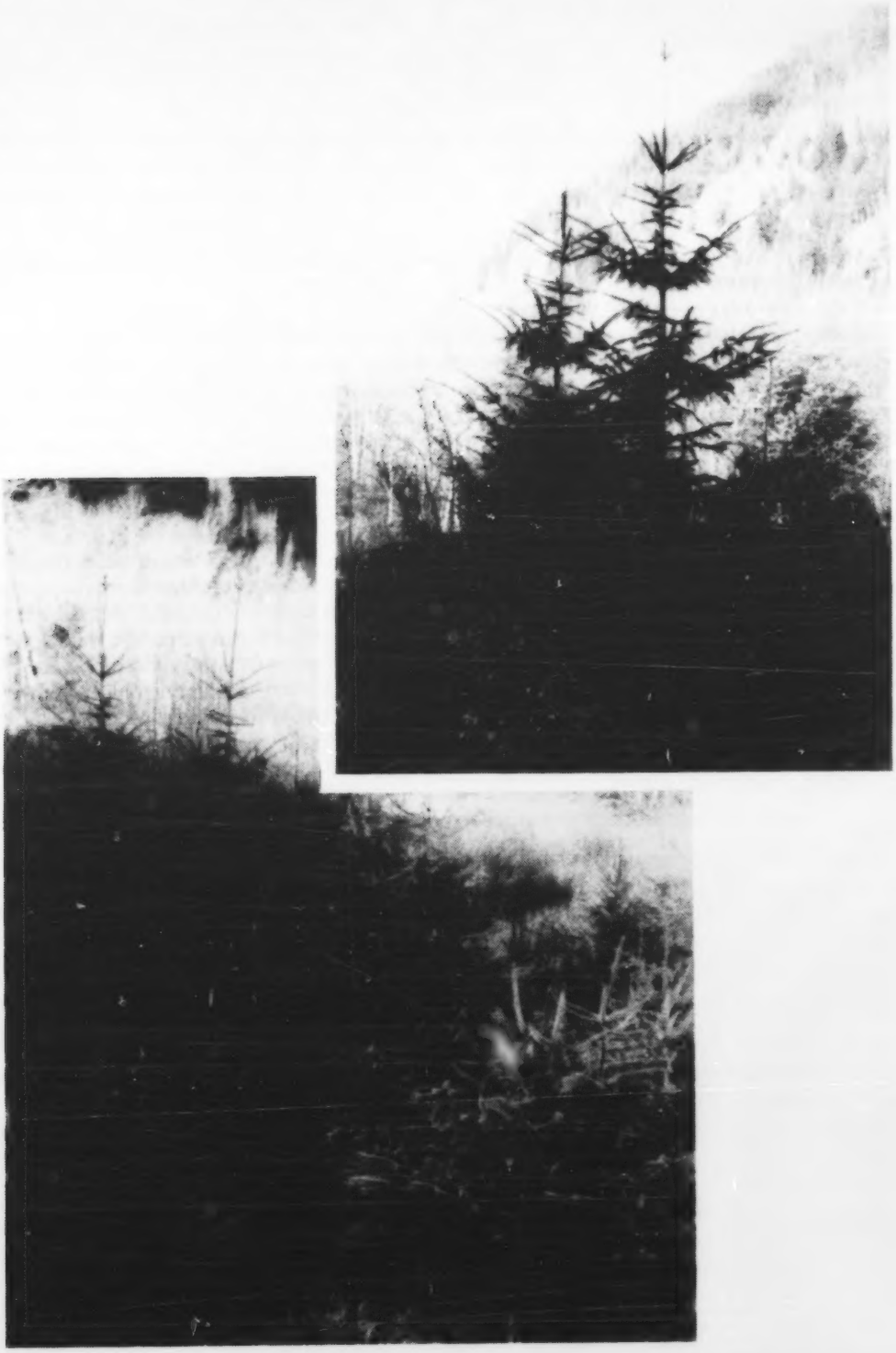

FIGURE 6. View of resistant (Haney source) vs. susceptible clones.

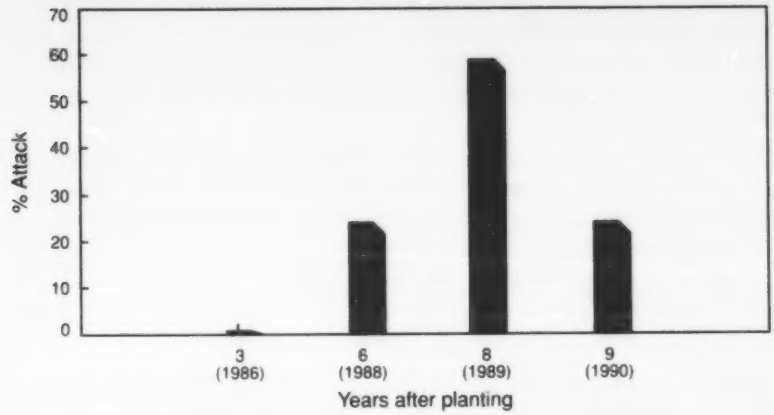

FIGURE 7. Percent of grafts attacked at different ages at Fair Harbour.

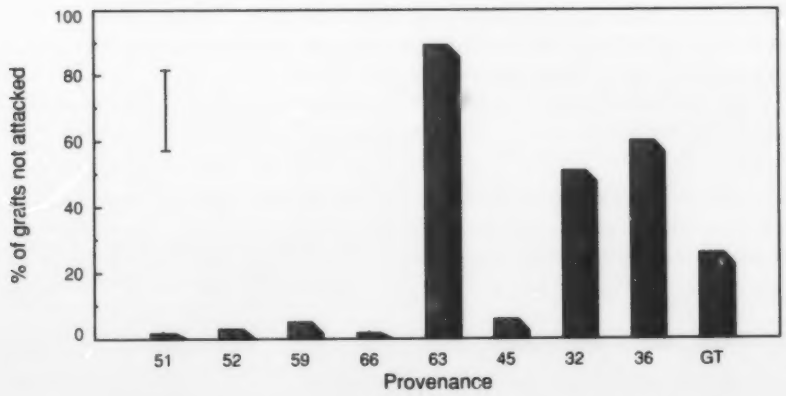

FIGURE 8. Provenance differences in percent of grafts not attacked at Fair Harbour. Barred line scaled to 1 LSD at 0.05 level.

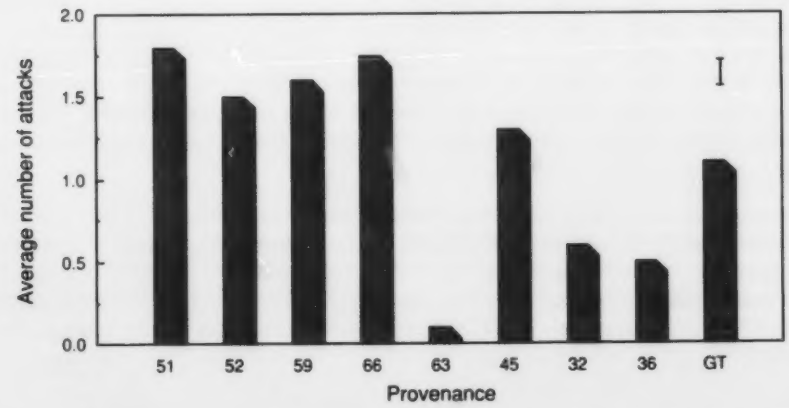

FIGURE 9. Provenance differences in average number of attacks per graft at Fair Harbour. Barred line scaled to 1 LSD at 0.05 level.

Utilization of Resistant Sources

Evidence of genetic resistance to the white pine weevil has been recently reported in interior spruce (Kiss and Yanchuk 1991) and Sitka-white spruce hybrids (Mitchell *et al.* 1990). Both reportedly have high repeatability of weevil resistance in different test site environments, suggesting a strong genetic component. Genetic basis in weevil resistance is evident.

The Haney and Big Qualicum provenances offer potential seed sources for reforestation in the high hazard zone (Figure 2), where planting of Sitka spruce is virtually non-existent at present. They are not only highly resistant to weevil, but also fast growing. At weevil-free sites, on the Queen Charlotte Islands for example, they grew as fast as did any lower coast provenance.

Use of wind-pollinated seeds from natural stands of the resistant provenances offers the quickest and cheapest way to use these resistant seed sources. However, the level of resistance of natural seeds will probably not be as high because of pollination by susceptible pollen sources.

Vegetative propagation of resistant genotypes is an effective way to capitalize on genetic resistance (Gerhold 1966), if vegetative propagation is feasible and economical. In Sitka spruce, techniques for rooting cuttings on a large scale have been developed, and field performance of cuttings is no different from that of seedlings (Mason and Gill 1986). Mass production of rooted cuttings using the concept of a hedging orchard offers high potential to produce a quantity of resistant stock in a short time (van den Driessche 1983). One drawback is that effective control of maturation in the long term has not yet been worked out (Mason and Gill 1986). New technology, such as somatic embryogenesis (Webster *et al.* 1990), cannot be effective until we know the mode of genetic inheritance that would allow the re-construction of genetic resistance after sexual recombination. It seems that, with the available propagation techniques at present, the hedging orchard offers the only practical way to mass produce rooted cuttings of resistant stock in the short term. The hedging orchard should be established at the same time as clonal testing so that when resistant clones are identified in about 5 years, the hedging orchard is ready for harvesting a large quantity of cuttings.

Selection and clonal screening of resistant genotypes have been in progress since 1989. A total of about 250 putatively resistant trees have been selected in both provenance test plantations and natural stands of resistant provenances. Clonal tests using grafts will be established in 1991 and 1992. About 50 resistant clones are expected to be released for operational use in 1996-97. A hedging orchard is being planned.

Long-Term Implications and Research Needs

The frequent breakdown of genetic resistance experienced with annual crops and the ability of insects to evolve resistance to insecticides have changed the philosophy of breeding for genetic resistance in forest tree species. It is an established principle that host plants and insects co-evolve interactionally; insects will eventually evolve to overcome the resistant mechanism of the host plants, if host resistance imposes severe enough selection pressure (Futuyma 1986). Long rotations of tree crops seem to make ineffective the "arms race" approach practised in breeding resistant agriculture crops. Bingham (1977), after decades of breeding for western white pine blister rust resistance, advocates breeding for long-term stabilized resistance. However, effective management of long-term genetic resistance requires knowledge about the physiological and chemical mechanisms of host preference, about the genetic mode of these mechanisms, and about the interaction of genetic resistance with silvicultural systems (Bingham 1977; Raffa 1989). Research is urgently needed in these areas.

Considerable research has been done on weevil-feeding mechanisms related to host morphological and chemical stimulants or deterrents at species level (Wood 1987). Attempts to determine the genetic basis of feeding mechanisms, however, is a recent undertaking. For example, a monoterpene profile has been used as an indicator of weevil resistance in Sitka spruce (Brooks *et al.* 1987). Reliable indicators of morphological, physiological, and chemical traits can greatly facilitate long-term selection and breeding for genetic resistance to the white pine weevil.

Resistance to the white pine weevil likely involves a variety of genetic systems as found in major forest disease (Bingham *et al.* 1971). Resistance shown by Sitka-white hybrids (Mitchell *et al.* 1990) may involve a genetic system different from that in "pure" Sitka spruce, since both Sitka and white spruce are susceptible to the white pine weevil. A synthetic variety containing diverse genetic systems of resistance may run a low risk of quick breakdown (Bingham 1977). Also, little is known in tree-insect systems about the mode of genetic transmission of resistance from parents to their offspring. Lack of knowledge on the mode of inheritance will hinder progress in long-term breeding for genetic resistance.

Silvicultural treatments such as shading (McLean 1989) and spacing (Alfaro and Omule 1990) have shown promising results to reduce weevil impact. But we know nothing about how genetically resistant trees would interact with these treatments. Deployment of genetically resistant trees has to be compatible with silviculture systems and other pest management measures (Bingham 1977; Raffa 1989) to maximize the benefits of pest control and to reduce the risk of inadvertent deleterious effects of resistant trees on the forest ecosystem.

Planting of Sitka spruce will continue to be limited mainly to the weevil-free sites (e.g., on the Queen Charlotte Islands) unless weevil damage can be effectively controlled. Genetic resistance can no doubt be an effective tool in controlling weevil. Long-term benefits from genetic resistance cannot be fully realized unless we understand the mechanism of genetic resistance, the mode of inheritance, and the integration of resistant trees with silviculture systems.

APPENDIX 1. Descriptions about test sites

Site	Test series	Lat. °N	Long. °W	Elev. (m)	BGU	Soil and topography
Juskatla	4	53°34'	132°20'	20	CWHwh1	Flat valley bottom, clay soil, restrictive drainage
Rennel Sound	4	53°23'	132°28'	50	CWHvm	Flat lower slopes, deep silt loam
Area 1, Q.C.I.	1	53°33'	132°20'	460	CWHwh2	2 blocks on SE facing steep hill (25-30%); 4 blocks on E facing very steep slope (40-45%); loamy but rocky soil
Area 2, Q.C.I.	1	53°31'	132°11'	33	CWHwh1	Flat lowland, deep loamy soil
Area 3, Q.C.I.	1	53°24'	132°16'	85	CWHwh1	3 blocks on flat lowland, deep loamy soil; 2 blocks on N facing lower slope (30-45%)
Area 4, Q.C.I.	1	53°22'	132°16'	100	CWHwh1	3 blocks on low flat land, deep loamy soil, wet spots with surface water year- round; 2 blocks on SW facing steep hill (45-50%), gravel sandy loam soil
Area 5, Q.C.I.	1	53°08'	132°01'	450	CWHwh2	Flat land in a bog
Dragon Lake	3	55°19'	128°58'	210	ICHmc3	Flat valley bottom, clay soil
Nass	3	55°04'	129°26'	15	CWHvm	Flat valley bottom, deep silt loam
Maroon Creek	3	54°46'	128°39'	600	CWHws2	Gentle lower slope (10-20%), gravel soil
Kitimat	4	54°12'	128°33'	100	CWHws1	Flat alluvial terrace, deep rich silty clay soil
Holberg	3	50°44'	128°07'	60	CWHvh1	Flat valley bottom, clay soil of marine origin with large size stone outcrop
Head Bay	4	49°48'	126°28'	15	CWHvm1	Flat valley bottom, silty loam to clay soil of marine origin
Sayward	2	50°13'	125°45'	75	CWHxm2	Flat valley bottom, sandy loam
Fair Harbour	C	50°03'	127°04'	20	CWHvm1	Flat valley bottom, silty loam

Q.C.I. = Queen Charlotte Islands
C = clonal test

APPENDIX 2. Information about provenance origin

Provenance code IUFRO	Local	Location	Zone[a]	Lat°N	Long°W	Elev. (m)	Biogeoclimatic unit
3021		Yakutat, AK		59°31'	139°42'	12	CWHvh
3024	28	Duck Cr., AK	L	58°22'	134°35'	30	CWHwm
3025	27	Ohmer Cr., AK	L	56°35'	132°44'	0-15	CWHvh
3026	11	Derrick Lk., BC	X	55°41'	128°41'	240	ICHmc2
3027	24	Craig, AK	L	55°30'	133°08'	0	CWHvh
3028	25	Old Hollis, AK	L	55°28'	132°40'	0	CWHvh
3029	05	Cranberry R., BC	X	55°28'	128°14'	510	ICHmc3
3030	26	Ward Lk., AK	L	55°25'	131°42'	15	CWHvh
3031	12	Dragon Lk., BC	X	55°21'	128°57'	255	ICHmc3
3032	06	Kitwanga, BC	X	55°10'	127°52'	660	ICHmc3
3033	13	Zolap Cr., BC	X	55°09'	129°13'	15	ICHmc3
3034	14	Fulmar Cr., BC	X	55°09'	128°58'	390	ICHmc3
3035	23	Moss Point, AK	L	55°02'	131°33'	0	CWHvh
3036	18	Cedarvale, BC	X	55°01'	128°19'	240	ICHmc3
3039	10	Kitsumkalum Lk., BC	X	54°43'	128°46'	135	CWHws1
3040	07	USK Ferry, BC	X	54°38'	128°24'	135	CWHws1
3041	08	Shames, BC	X	54°24'	128°57'	30	CWHws1
3042	19	Kasiks R., BC	X	54°17'	129°25'	30	CWHvm
3044	21	Inverness, BC	L	54°12'	130°15'	0-30	CWHvh
3045	15	Aberdeen, BC	X	54°12'	129°55'	0	CWHvh
3046	09	Wedeene R., BC	X	54°08'	128°37'	165	CWHvm
3047	20	Humpback Cr., BC	L	54°02'	130°22'	300	CWHvh
3048	40	Masset Sd., BC	L	53°55'	132°05'	0	CWHwh1
3049	39	Link Rd., BC	L	53°30'	132°10'	90	CWHwh1
3050	38	Copper Cr., BC	L	53°08'	131°48'	75	CWHwh1
3051	37	Moresby Camp, BC	L	53°03'	132°04'	60	CWHwh1
3052	36	Tasu Cr., BC	L	52°52'	132°05'	15	CWHvh
3053	35	Jedway, BC	L	52°17'	131°13'	15	CWHwh1
3056	34	Holberg, BC	L	50°37'	128°07'	30	CWHvh1
3058	04	Salmon Bay, BC	H	50°23'	125°57'	0	CWHxm2
3059	32	Fair Harbour, BC	M	50°03'	127°02'	30	CWHvm1
3060	02	Squamish R., BC	H	49°53'	123°15'	30	CWHdm
3061	33	Tahsis Inlet, BC	M	49°50'	126°40'	0	CWHvm1
3062	03	Big Qualicum R., BC	H	49°23'	124°37'	0	CDFm
3063	29	Haney, BC	H	49°14'	122°36'	90-300	CWHdm
3064	01	Vedder, BC	H	49°07'	121°56'	30	CWHdm
3065	31	Port Renfrew, BC	H	48°35'	124°24'	0-15	CWHvh1
3066	30	Muir Cr. Sooke, BC	H	48°23'	123°52'	0	CWHxm2
3073	41	Blenheim Mt., BC	M	48°54'	124°57'	180-240	CWHvm1
3003		Forks, WA		48°04'	124°18'	120-150	CWHvm1
3008		Hoquiam, AK		47°05'	124°03'	5	CWHvm1
3012		Necanicum, OR		45°49'	123°46'	45	CWHvm
3018		Brookings, OR		42°15'	124°23'	90	CWHvm

[a] L = low, M = medium, and H = high weevil hazard zone (Heppner and and Wood, 1984); X = Sitka and white spruce hybridization zone (Woods, 1988).

APPENDIX 3. Provenance means of number of weevil attacks per tree, percent of trees attacked at least once, and total height at Sayward, assessed in 1988 (15th-year after planting)

Provenance		No. of trees		% Trees attacked	Total no. attacks	No. attacks in severe patch[b]	Height (m)
IUFRO no.	Zone[a]	living	attacked				
24	L	133	105	79	1.5	1.7	2.8
25	L	79	70	89	1.9	1.9	3.1
26	X	131	72	55	0.9	1.3	3.7
27	L	159	136	86	1.7	1.7	3.0
28	L	194	167	86	1.8	2.3	3.1
29	X	158	95	60	1.1	1.3	3.5
30	L	62	50	81	1.8		3.1
31	X	82	60	73	1.4	1.5	3.9
32	X	93	51	55	1.1	1.1	3.5
33	X	115	94	82	1.5	1.8	3.4
34	X	206	151	73	1.4	1.6	3.6
35	L	87	74	85	1.6	1.9	3.1
36	X	134	66	49	0.9	0.8	3.5
39	X	107	82	77	1.7	1.8	3.9
40	X	133	91	68	1.4	2.1	3.7
41	X	115	88	77	1.5	1.2	3.3
42	X	182	135	74	1.3	1.5	3.3
44	L	119	85	71	1.2	1.7	3.1
45	X	131	96	73	1.2	1.4	3.1
46	X	126	76	60	1.2	1.5	3.8
47	L	41	35	85	1.9		2.7
48	L	165	147	89	2.2	2.2	3.5
49	L	94	87	93	2.1	2.1	3.4
50	L	23	13	57	1.0		3.4
51	L	98	87	89	2.2	2.5	3.4
52	L	110	83	75	1.5	1.9	3.2
53	L	83	64	77	1.9	2.3	3.1
56	L	80	76	95	2.4	2.6	3.3
58	H	252	201	80	1.7	2.2	3.9
59	M	251	216	86	1.8	2.0	4.0
60	H	176	121	69	1.2	0.9	4.2
61	M	39	34	87	1.7		3.9
62	H	234	186	79	1.7	2.1	5.0
63	H	81	35	43	0.8	0.6	5.5
64	H	15	11	73	1.4		4.5
65	H	80	68	85	1.7	2.0	3.7
66	H	64	49	77	1.5	1.8	4.3
73	M	79	72	91	2.4	2.6	4.1
Total (mean)		**4511**	**3429**	**76**	**1.5**	**1.8**	**3.6**

[a] L = low, M = medium, and H = high weevil hazard zones; X = Sitka and white spruce hybridization zone.
[b] Only for trees in lows with average number of attacks per tree higher than 1.6.

APPENDIX 4. Provenance means of percent of trees attacked and number of attacks per tree from 1984 to 1989 (10th- to 15th-year), and 15-year height at Head Bay, Kitimat, and Nass

Provenance	Head Bay			Kitimat			Nass		
	% Trees attacked	No. of attacks	Height (m)	% Trees attacked	No. of attacks	Height (m)	% Trees attacked	No. of attacks	Height (m)
12 Necanicum, OR	95	1.3	6.3	82	2.8	4.5	95	2.0	4.1
08 Hoquiam, WA	84	1.1	5.7	96	2.8	4.7	–	–	–
03 Forks, WA	86	1.2	5.7	98	2.7	4.8	99	2.1	4.0
62 Big Qualicum, BC	39	0.4	6.4	69	1.2	5.4	65	0.9	5.2
61 Tahsis, BC	–	–	–	–	–	–	97	2.0	3.7
56 Holberg, BC	83	1.1	4.4	94	2.7	4.2	95	1.8	3.7
49 Link Rd., BC	96	1.3	4.7	90	3.2	4.0	96	2.2	3.8
44 Inverness, BC	76	0.9	4.3	96	2.5	3.5	100	2.0	3.5
40 USK Ferry, BC	46	0.5	4.2	87	1.7	4.6	–	–	–
32 Kitwanga, BC	–	–	–	–	–	–	41	0.8	4.9
30 Ward L., AK	79	0.9	3.7	97	2.4	3.4	–	–	–
24 Duck Cr., AK	69	0.7	3.5	93	2.7	3.1	–	–	–
21 Yakutat, AK	–	–	–	–	–	–	88	1.4	2.6
Mean	**76**	**1.0**	**4.9**	**90**	**2.5**	**4.2**	**85**	**1.7**	**4.0**

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